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THE ANATOMICAL CHANGES IN THE STRUCTURE OF THE VASCULAR CYLINDER INCIDENT TO THE HYBRIDIZATION OF CATALPA.

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IN 1889 Prof. C. S. Sargent published an account of an interesting and newly observed case of hybridization between two species of Catalpa which he designated as Catalpa × J. C. Teas in reference to the origin of the tree in the nursery of Mr. Teas at Carthage, Missouri.[1] The account referred to states that *Catalpa kœmpferi* was planted in 1864 in a nursery containing *C. speciosa* and *C. bignonioides*. Eventually the first species produced a single pod of seeds which were wholly unlike anything hitherto known. When these seeds were planted, they produced a tree almost intermediate in character between *C. kœmpferi* and one of the American species. Mr. Teas was of the opinion that the cross was with *C. speciosa*, while Prof. Sargent considered *C. bignonioides* as the other parent, basing his conclusion upon the fact that *C. speciosa* flowers two to three weeks earlier than *C. kœmpferi*, while the flowers of *C. big-*

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[1] *Garden and Forest*, vol. 2, 1889, p. 303.

nonioides are contemporaneous with those of the Japanese species. No other evidence has been forthcoming since then, so far as I am aware, and the real American parentage of a most noteworthy addition to the ornamental trees of this country still remains in doubt. Within the last twelve years, opportunities have been presented to inquire into the evidence which might be secured from an anatomical point of view, and to determine to what extent the external alterations attendant upon hybridization correspond with internal structural changes. It was felt that the answer to this question might very largely contribute to a solution of the difficult problems relating to the origin of species by either mutation or hybridization, and admit of a more precise limitation of the characters which define a species. The

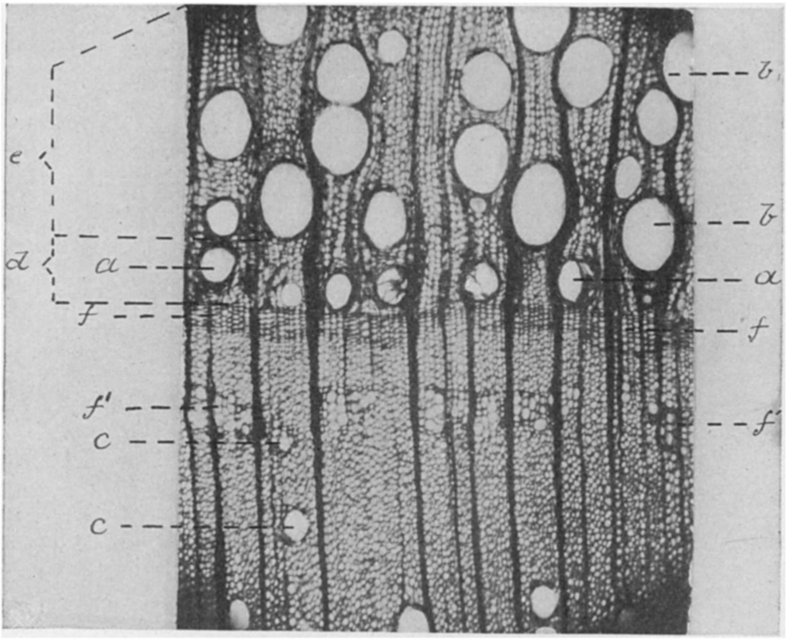

FIG. 1.—*Catalpa teasi.* Transverse section, × 44. *a*, vessels of the primary zone showing small size and few thyloses; *b*, vessels of the secondary zone abruptly much larger and chiefly devoid of thyloses; *c*, the greatly reduced and widely scattering vessels of the last growth of the season; *d*, narrow zone of thin-walled cells of the spring wood; *e*, cells of the summer wood; *f*, zone of spiral and scalariform tracheids forming a limiting layer of uniform width and chiefly without radial extensions, but repeated at *f'* in a second zone centering in the greatly reduced and more numerous vessels.

importance of this latter point of view was the more strongly impressed upon me because, in the course of studies relating to the recognition of species among the North American Coniferales as determined by the anatomy of the woody axis, I had been obliged to adopt the working hypothesis that there are no varietal forms in the sense commonly employed and as expressed in variations of the external organs, and that where these variations arise, they define species as certainly, though not as conspicuously as in other cases. Fortunately I already had in my possession, wood of *C. bignonioides* and *C. speciosa*, while fresh material of the latter was also obtained from trees growing in the grounds of McGill University. About twenty years ago, a specimen of Teas hybrid was planted out in the College grounds, and it has proved perfectly hardy up to the present time, though two other specimens planted about eight years ago were completely killed during the two winters of 1902 and 1903. Recently Mr. Burton Landreth of Bristol, Pa., who possesses a growth of *C. kæmpferi*, very kindly sent me a specimen of wood, and it has thus become possible to bring the wood structure of the hybrid into direct comparison with that of the three species among which its parents are to be found. Later specimens of *C. kæmpferi* from Mr. J. G. Jack of the Arnold Arboretum, have also enabled me to institute more extended comparisons. Before proceeding to a discussion of the results obtained, it will be desirable to recall the essential features of the hybrid as given by Sargent, and to see the direction in which such evidence tends.

"The hybrid is an erect, vigorous and rapid growing tree, with the thin, scaly bark of the American species. The leaves of this tree are much larger than those of either of its parents, having, when they first appear, the velvety character and purple color peculiar to those of the Japanese plant, and the reddish spot at the insertion of the petiole with the leaf blade which characterizes that species. They more generally resemble those of the Japanese species in shape, color and texture, while the pubescence which covers the lower surface is almost intermediate in character between that of the American and of the Japanese species. The inflorescence is much larger than that of the American or of the Japanese plants, being fully twice as large as that of *C. bignonioides* and more than three times the size of *C. kæmpferi*. The flowers are intermediate in size; in color and markings they most nearly resemble those of the American species, although a tinge of yellow in the throat of the corolla points to their Japanese descent. The fruit of the hybrid is almost intermediate in size between those of the two parents, as are the seeds, which are perfectly fertile and often reproduce the original form in every particular. When, however, seedlings show a tendency to vary from the original form, the variation is generally in the direction of the Japanese rather than of the American parent."

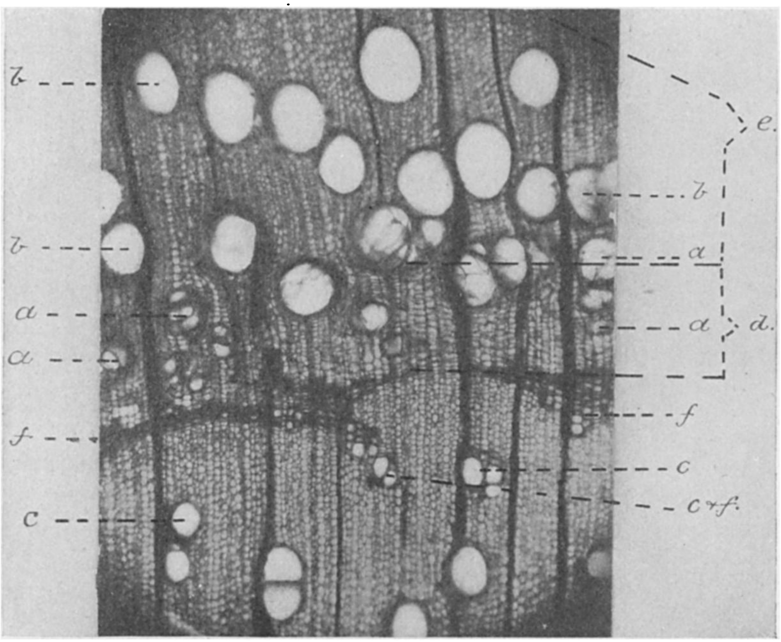

FIG. 2.—*Catalpa kæmpferi.* Transverse section, × 44. *a*, vessels of the primary zone with thyloses; *b*, vessels of the secondary zone showing great increase in size and diminution of the thyloses; *c*, vessels of the last of the season's growth; *d*, thin-walled cells of the spring wood; *e*, smaller and somewhat thicker-walled cells of the summer wood; *f*, zone of spiral and scalariform tracheids limiting the growth ring and showing radial extensions in connection with the last small vessels.

"The hybrid is a more vigorous tree than either of the American or the Japanese species, and it grows rather more rapidly.

Of its value as an ornamental tree there can be no doubt. Its larger size and more rapid growth, its better habit and more showy inflorescence, make it a far more valuable ornamental tree than the Japanese species; it is more hardy than either of the North American species, and although the flowers are smaller, the panicles and the number of the individual flowers are much larger." The inflorescence of the hybrid is also remarkable for its prolonged duration which extends from June until September as presented by specimens grown here.

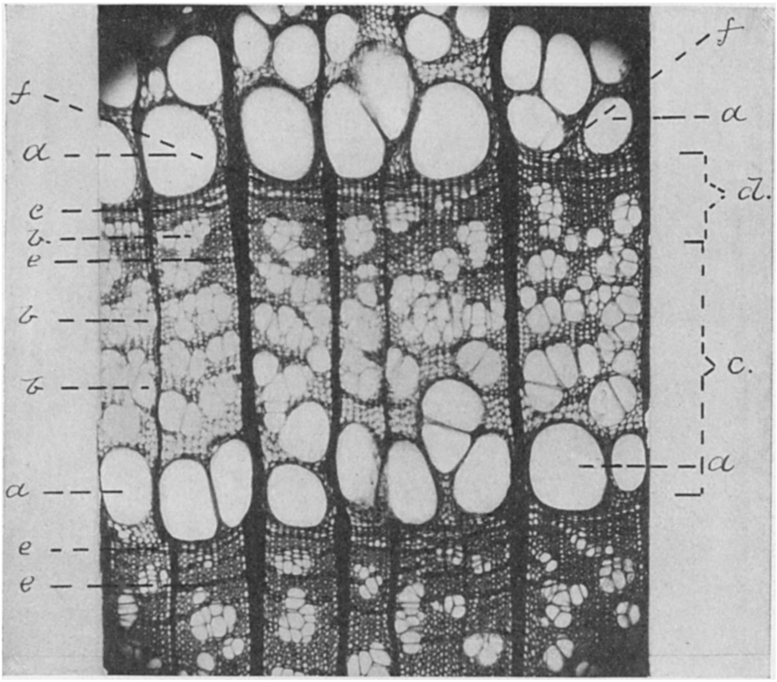

FIG. 3.—*Catalpa speciosa.* Transverse section, × 44. *a*, very large vessels of the primary zone without thyloses; *b*, small and much compounded vessels of the secondary zone, rather abruptly terminated in the outer region of the growth ring; *c*, the broad zone of the spring wood; *d*, the narrow zone of the summer wood; *e*, tangential and concentric bands of resinous wood parenchyma; *f*, the narrow, limiting zone of wood tracheids.

We may now turn to a study of the internal structure of the hybrid and of the three related species in order to determine (1) if the crossing has made an impress upon the anatomical structure, or if it is simply expressed in external characteristics; (2)

if there is any anatomical evidence which will determine the species with which *C. kæmpferi* was crossed; and (3) if this evidence bears any relation to the fixity of the form and in any way defines a new species. To this end it will be necessary to elaborate the separate diagnoses and compare them with one another, as also with differences in color, form, and texture as applicable to the leaves and flowers.

TEAS HYBRID (Figs. 1, 5).

Transverse.— Growth rings very broad, the spring wood thin but the distinction between it and the summer wood not clearly recognizable. The wood cells of the earliest growth sometimes tangentially elongated, in more or less obvious radial rows and rather large with rather thin walls; the structure of the later growth chiefly the same throughout the growth ring, the cells hexagonal, in somewhat definite radial rows, not thick-walled, very variable in size with little or no diminution toward the outer limits. Wood parenchyma confined to the composition of the vessels and to the earliest spring wood where the cells become distinctly larger and more resinous. Wood tracheids prominent, squarish, in very definite radial rows, forming a narrow zone of about six elements on the outer face of the growth ring, but locally extended radially inward opposite the smaller vessels with which they join so as to form tracts of variable width; also uniting with the smaller vessels to form a second and more internal, discontinuous zone of very irregular width and form. Vessels at first medium and forming a single layer with strongly developed thyloses; becoming abruptly larger in the second layer, radially oval or oblong and chiefly single, but sometimes 2–3 compounded radially and tangentially and largely devoid of thyloses; soon diminishing in size and number, radially compounded and much scattered in irregular groups of 2–6 throughout the growth ring, finally reduced somewhat abruptly in the last growth of the season to the dimensions of tracheids with which they coalesce into irregular tracts. Medullary rays prominent, numerous, somewhat resinous especially in the spring wood, 1–3 cells wide, distant upwards of 178 μ.

Radial.— Medullary rays somewhat resinous, the cells straight, rather uniform in height, very variable in length and from 3–4 times longer than high, or again very short and much higher; the upper and lower walls rather thick and finely pitted; the terminal walls straight or curved and finely pitted; the lateral walls not pitted except opposite vessels and then with small, numerous, oval and unequal pits. Tracheids of the limiting zone with spiral and scalariform structure which merges into 1–2 rows of simple pits on the radial walls. Wood parenchyma somewhat resinous and exceedingly variable; when adjacent to the spiral tracheids of the summer wood, very narrowly cylindrical, when adjacent to vessels, usually short cylindrical and bearing numerous transversely oval or oblong pits on the radial walls. Vessels often much shorter than broad, the radial walls with multiseriate, hexagonal pits throughout, the orifice transversely oblong.

Tangential.— Rays very numerous, low to medium, 1–3 cells wide, somewhat resinous; the cells chiefly oblong, rather thin-walled, those of the extremities much larger and more variable. Vessels with multiseriate, hexagonal or more commonly oval, bordered pits which frequently become simple, distant, and transversely oval or oblong. The tangential walls of the wood parenchyma with numerous transversely oval or oblong pits. Tracheids often devoid of spiral and scalariform structure which is replaced by upwards of 3 rows of simple pits.

The features thus described will be found in the figures of the transverse and longitudinal sections. As one of the parents of this hybrid is known to be *C. kæmpferi*, its diagnosis may be

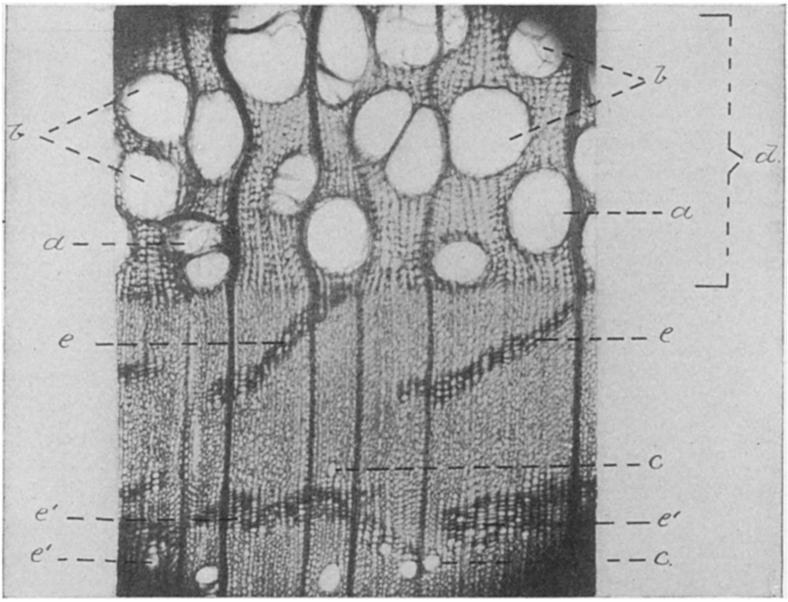

FIG. 4.— *Catalpa bignonioides.* Transverse section, × 44. *a*, very large vessels of the primary zone showing few thyloses; *b*, the vessels of the secondary zone chiefly without thyloses; *c*, the greatly reduced and distant vessels of the summer wood which do not appear prominently within a wide zone; *d*, the broad zone of the thin-walled cells of the spring wood; *e*, diagonally radial tracts of spiral and scalariform tracheids connecting with the outermost and most reduced vessels; *e′*, tangentially extended tracts of tracheids centering in larger vessels and forming an almost continuous, secondary zone.

given and brought into direct comparison in order to ascertain what characters have been derived from it. By elimination it will then be possible to refer the remaining characters to either *C. speciosa* or *C. bignonioides*.

C. kæmpferi (Figs. 2, 6).

Transverse.— Growth rings very broad. Differentiation of the spring and summer woods well defined (?), the latter constituting the bulk of the growth ring and defined by a somewhat abrupt transition in the form, size, and thickness of wall of the component cells. The spring wood composed of large, variable, squarish-hexagonal and tangentially elongated, non-resinous, and thin-walled cells which form a limiting zone external to the previous growth ring; soon replaced by the somewhat abruptly smaller, rather thin-walled, hexagonal and radially elongated cells of the summer wood which diminish almost imperceptibly toward the outer face of the growth ring. Wood parenchyma strictly confined to the composition of the vessels. Tracheids conspicuously squarish, rather uniform, in regular radial rows, more or less resinous, rather thick-walled and forming a limiting layer upwards of six cells thick on the outer face of the summer wood, or opposite the most recently formed small vessels, joining with the latter to form radially extended tracts of irregular form and extent, or even forming detached groups centering in small vessels, so as to form a second zone of imperfect development. Vessels somewhat numerous and scattered throughout the growth ring; those of the early spring wood with strongly developed thyloses; at first rather small, numerous and round, but abruptly enlarging with the corresponding transition from the spring to the summer wood cells, and becoming oval or radially extended and 2–3 compounded in radial series, predominant; again abruptly reduced in size and number, sometimes radially 2–3 seriate, and thence continuing without much variation to the region of the outer summer wood where they are once more abruptly reduced in size and there give rise to the terminal layer of tracheids. Medullary rays prominent, sparingly resinous, 1–3 cells wide, distant upwards of 427 μ.

Radial.— Medullary rays sparingly resinous; the cells within the region of the early spring tracheids chiefly short; isodiametric; the upper and lower walls rather thick and strongly pitted; the terminal walls thicker and more strongly pitted; the lateral walls with numerous small pits in more or less definite radial series; in older parts of the growth ring the cells increase greatly in length, except the marginal ones which remain short and become much higher, the pits on the lateral walls opposite vessels become much larger and oval. Wood parenchyma of the spring wood composed of short and thin-walled cells which bear rather numerous, transversely oval, simple pits on the radial walls; those of the vessels of later growth much longer and narrower. Tracheids of the summer wood narrow, spiral, scalariform, and pitted, and showing all transitional forms from simple spirals to hexagonal bordered pits in 1–3 series. The radial walls of the vessels with numerous hexagonal pits having rather large, transversely oval or oblong openings.

Tangential.— Medullary rays rather numerous, resinous, low to medium and 1–3, chiefly 2 cells wide; the cells rather thick-walled, hexagonal. Tangential walls of the vessels with numerous and variable, transversely oval, oblong or long linear, often simple pits. The tangential walls of the spring parenchyma with numerous round or transversely oval, chiefly simple pits; those of the early spring wood cells with transversely linear, narrow and rather numerous pits.

A comparison of the transverse and tangential sections for this species, with those for the hybrid, makes the general relations of the two very obvious, but a more critical examination of them is necessary. In each case the wood is characterized by the great breadth of the growth ring. In *C. kæmpferi*, the thin-walled spring wood constitutes a rather narrow zone representing but a small volume of the total growth for the season. Precisely the same is also true of the hybrid with the difference that the volume is reduced to about one half what is to be found in the former, showing the definite influence of one parent. In each case the wood parenchyma is confined to the composition of the vessels or to the earliest spring wood, and there is no feature in them which can be directly ascribed to *C. kæmpferi*. A very definite connection between *C. kæmpferi* and the hybrid, appears in the distribution of the tracheary tissue which, in the latter, forms a well defined limiting layer occupying the same position as in the former but characterized by greater uniformity of width. This is undoubtedly due to *C. kæmpferi* in the first instance, but ultimately it is to be regarded as a resultant effect from the interaction of the two parents as will appear later. In addition to the limiting zone of tracheids which sometimes extends radially inward as in *C. kæmpferi*, though not generally to the same extent or so frequently, it is to be noted that in the hybrid there is a second and more internal zone of tracheary tissue which centers in the small vessels of the outer summer wood and which forms tangentially extended tracts of a very well defined character. This feature is one of the most prominent structural changes, and it points with great force and directness to the influence of some other parent than *C. kæmpferi*, although this has also exerted an influence. In the distribution, size, and character of the vessels, there are but few features which serve to guide us in forming a conclusion, but it will be noted that the conspicuous thyloses of *C. kæmpferi* have practically disappeared in the hybrid though retained in the initial row of vessels which have increased slightly in size and are confined to a much narrower, radial zone. This points without doubt to the influence of the other parent. In the outer regions of the growth ring, the vessels are seen to be conspicuously smaller and on the

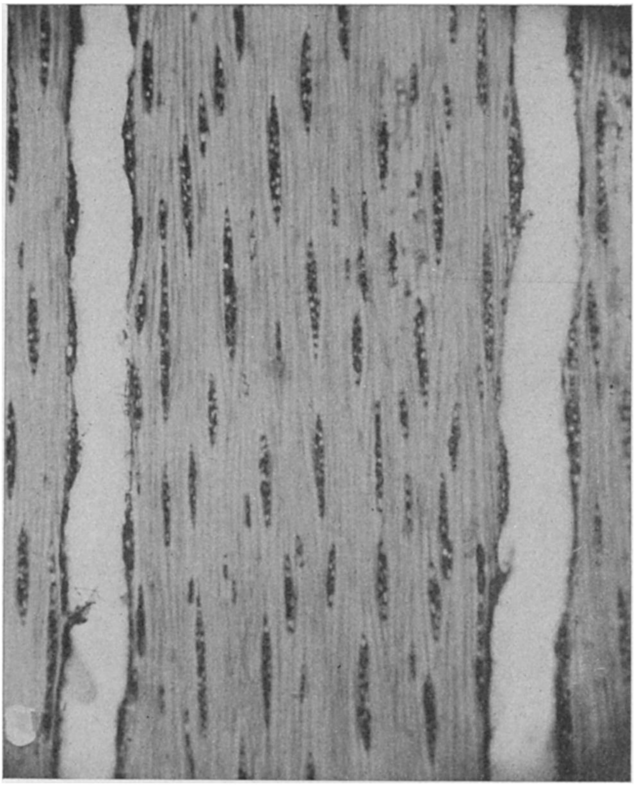

FIG. 5.—*Catalpa teasi.* Tangential section, × 61. Showing vessels with few or no thyloses, and the rather numerous and medium rays of lenticular form, 2–3 cells wide.

whole, more scattering in the hybrid than in *C. kæmpferi*, a feature undoubtedly derived from the other parent. The medullary rays offer no evidence of value in favor of either parent, since in each case they present the same features of structure.

In the structure of the medullary ray as presented in radial section, some features are worthy of consideration. The generally short, isodiametric cells of *C. kæmpferi* are more commonly replaced in the hybrid by longer and very variable cells, the upper, lower, and terminal walls of which are marked by fine pits, all of which features must have been derived from another parent than *C. kæmpferi* in which the walls are distinguished by coarse pits. While in the latter species the pits on the lateral walls of the cells are rather large and oval, in the hybrid they become small, numerous, and unequal. In each case the spiral and scalariform tracheids of the summer wood show transitional forms leading to the development of pits, but while in *C. kæmpferi* these latter structures are hexagonal, bordered, and in 1–3 series, in the hybrid they are usually simple and in 1–2 rows only, thus showing a modification which must be attributed to the other parent.

In a tangential section the medullary rays correspond in approximate number and height, as also in the number of series of cells entering into their composition, but while in *C. kæmpferi* the cells are rather thick-walled and hexagonal, in the hybrid they are rather thin-walled and oblong, the marginal cells becoming much higher and more variable. From this comparison it is obvious that *C. kæmpferi* has influenced the hybrid in very definite ways, while it is equally clear that the latter presents a number of characteristics which could have been derived only from *C. speciosa* or *C. bignonioides*, and in order to determine which, we may next compare *C. speciosa*. An inspection of a transverse section of this wood shows that it possesses features of structure which are in very marked contrast to what may be found in either of the preceding species, but in order to make these differences clear, a diagnosis may be given before proceeding to a detailed comparison.

C. speciosa (Figs. 3, 7).

Transverse. — Growth rings narrow, rather uniform, consisting of about one half spring and one half summer wood distinguished by their variations in (1) size of cells, (2) the thickness of the walls, and (3) the disposition of the cells. Cells of the spring wood large, thin-walled, hexagonal or sometimes tangentially extended, in somewhat obvious radial rows; those of the summer wood hexagonal, uniform, thick-walled, smaller and *not at all* in radial rows. Wood parenchyma dark and resinous, the cells forming tangential and concentric series at frequent intervals, chiefly in the summer wood. Wood tracheids thin-walled, few, in two or three rows terminating the growth ring as a layer of uniform thickness. Vessels of the earliest spring wood at first very large, oval or round, rarely compounded, and chiefly devoid of thyloses; quickly reduced and soon compounded in radial and tangential series and finally reduced to about twice the diameter of the wood cells; very numerous throughout the growth ring to which they impart an element of great porosity. Medullary rays somewhat numerous, dark, 1–several cells wide, distant upwards of 445 μ.

Radial.— Wood parenchyma abundant, the cells in parallel rows, 14.6 μ to 100 μ wide; sparingly resinous, the radial walls with rather numerous, small and simple pits. Medullary rays sparingly resinous; the cells chiefly uniform in height except the marginal ones which are very variable, short in the summer wood and upwards of 2½ times the height, or in the spring wood several times longer than high, the upper and lower walls sinuately unequal, rather thick, conspicuously pitted; the terminal walls straight, strongly but rather finely pitted; the lateral walls devoid of pits except opposite vessels where they commonly show a fine sieve-plate structure or are otherwise numerously pitted. Vessels chiefly rather short but very variable, the terminal walls rather thick but not pitted; the radial walls with multiseriate, very variable, hexagonal, round, oval, transversely oval or oblong, often much elongated and distant pits, the orifice finally becoming a much elongated, narrow slit without a border, thus showing transitions into scalariform structure. Radial walls of the spring wood cells with rather small, longitudinally oblong pits in vertical series. Tracheids of the summer wood interspersed with wood parenchyma, the radial walls spiral and scalariform and merging into rather small, oval, bordered pits upwards of 5-seriate.

Tangential. — Medullary rays numerous, low to very high, often equal to 2 mm., dark, resinous, one to unequally multiseriate and upwards of 5 cells wide; the cells small, round or oval, thick-walled, variable, the terminal cells commonly oblong. Wood parenchyma of the spring wood composed of short cylindrical cells with square or fusiform ends, the tangential walls with numerous, multiseriate but small, transversely oval, bordered pits. Tangential walls of the vessels with numerous small, multiseriate, hexagonal or transversely oval, bordered pits.

A careful analysis of this diagnosis shows that the most marked deviations from the characters embodied in the hybrid, are to be found in (1) the growth rings which are always several times less in radial extent and far more porous, (2) in the character of the initial layer of vessels which are always very large and devoid of thyloses, (3) in the character of the vessels of later growth, which are always much compounded and much smaller, their reduction from those of the initial layer being abrupt, (4) in the presence of numerous resinous wood parenchyma cells which lie in definite, concentric zones of one cell in width, (5) in the tangential aspect of the medullary rays which are exceedingly variable in height, of very unequal width and upwards of

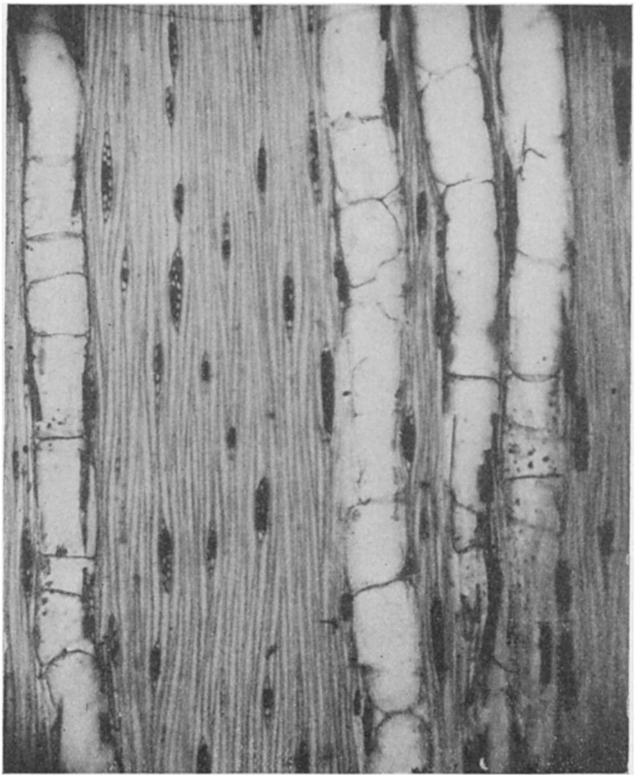

FIG. 6.— *Catalpa kæmpferi.* Tangential section, × 61. Showing vessels with numerous thyloses and the low, rather numerous rays of lenticular form, upwards of three cells wide.

5 cells wide. These features are of so pronounced a nature as to leave no doubt whatever as to the fact that *C. speciosa* is not in any way concerned in the production of the hybrid, since none of its characteristics are to be met with in the latter. It now becomes necessary to determine as a final factor, whether the features of the hybrid which we have already seen cannot be accounted for as being derived from *C. kæmpferi*, are in any way attributable to *C. bignonioides*.

C. bignonioides (Figs. 4, 8).

Transverse.— Growth rings very broad. The summer wood not sharply defined but distinguishable by (1) the smaller size of the wood cells, (2) the reduction of the vessels, and (3) the presence of groups or tracts of tracheids. Spring wood composed of large, variable, hexagonal, and tangentially elongated cells in somewhat obvious radial rows, the walls thin; soon replaced by the smaller and radially extended cells of the summer wood which diminish very gradually toward the outer limits of the growth ring. Wood parenchyma confined to the structure of the vessels. Tracheids rather thick-walled, non-resinous, squarish or tangentially extended, in radial rows confined to the outer portions of the growth ring where they form irregular and tangentially extended tracts of variable, often great extent in two series; the inner rather broad and strictly tangential, the rather large tracts more or less confluent and continuous, the outer formed of narrow, diagonal and chiefly free tracts projected inwardly from the outer limits of the growth ring. Vessels of the spring wood with strongly developed thyloses, at first large, oval or round, single and strongly predominant; soon becoming 2–3 compounded in radial series and steadily diminishing in size, shortly becoming single and more distant, and finally replaced wholly by groups of tracheids. Medullary rays prominent, 1–several cells wide, sparingly resinous, distant upwards of 462 μ.

Radial.— Medullary rays sparingly resinous; in the spring wood the cells are upwards of six times longer than high, the upper and lower walls very thin and barely pitted, the terminal walls thin and finely pitted, the lateral walls with occasional fine and simple pits; in the summer wood the cells are often not much longer than high, the upper and lower walls finally rather thick and strongly pitted, the terminal walls rather thick and finely pitted, the lateral walls when opposite vessels with rather small and commonly numerous, oval, simple pits in more or less definite radial series. Wood parenchyma of the first spring wood composed of short-cylindrical and rather broad cells, the radial walls with numerous, transversely oval or oblong, simple pits. The tracheids of the summer wood narrowly cylindrical and showing all transitional forms from spiral and scalariform to small, transversely oval, and simple pits, or 2-seriate hexagonal bordered pits. Radial walls of the cells of the summer wood commonly with small, lenticular pits showing a cross. Radial walls of the vessels with multiseriate, hexagonal or even transversely oblong, distant pits, the thyloses with distant, linear and simple pits.

Tangential.— Rays rather narrow, medium to somewhat high, upwards of 3-seriate, the cells all thin-walled, hexagonal. Tangential walls of the vessels with multiseriate, oval pits, the narrow, linear orifice of which is transverse and often exceeding the pit. Pits on the tangential walls of the spring wood parenchyma often simple and transversely oblong.

The growth rings of *C. bignonioides* are seen to be very broad, thus conforming to what also appears characteristic of *C. kæmpferi*, and what arises as a necessary resultant in the hybrid, but constituting a feature entirely wanting in *C. speciosa.* Thus it appears that the growth rings in *C. speciosa* are approximately only one fifth of the radial dimensions in either the hybrid or *C. bignonioides.* While in general terms this difference may be said to exist, it cannot be taken as a differential character of leading importance for the reason that under certain circumstances of growth, the hybrid may develop equally narrow rings. Putting this factor to one side, we then find that the structure of the growth ring affords a very definite means of determining any possible relationship. The region which I consider as probably representing the spring wood, is several times broader than in *C. kæmpferi*, and the contraction of this zone in the hybrid must be viewed as due to the direct influence of the latter species. The vessels of the early spring wood are large and they increase in size for some distance within the limits of the spring wood, so as to form a rather broad zone without any well defined distinction of a primary and secondary zone as appears in *C. kæmpferi* and more prominently in the hybrid, and it is probably correct to say that the limitation in size and distribution which is expressed in the latter, is the direct result of the dominating influence of the large vessels of *C. bignonioides.* The influence of the latter is also expressed in the general distribution of the vessels. In *C. kæmpferi*, *C. bignonioides*, and the hybrid, the vessels gradually diminish in size toward the outer limits of the growth ring, but a comparison of their distribution in the first and last shows that the hybrid occupies an intermediate position between the first two in such a manner as to show the direct influence of the latter in a reduction of both size and number in the outer summer wood. This feature is again correlated with the distribution of the tracheids. Our diagnoses have shown that in *C. kæmpferi* these elements form a limiting zone which is locally increased in thickness in a radial direction opposite the small vessels of the outer summer wood, with which they coalesce to form irregular tracts; or again centering in small vessels so as to form a second zone of small and rather distant tracts. The same feature appears also in *C. bignonioides* but in such a modified form as to constitute a distinc-

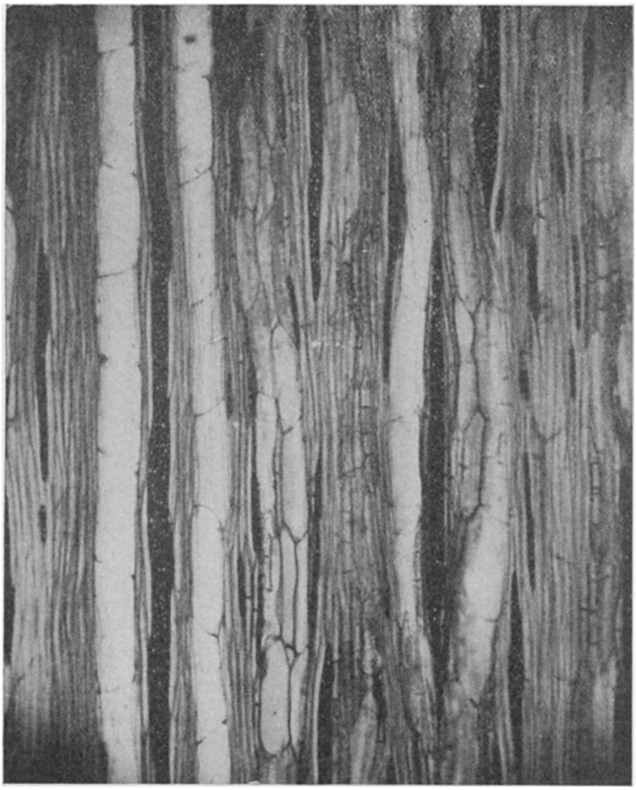

FIG. 7.—*Catalpa speciosa*. Tangential section, × 61. Showing the vessels with rather few thyloses and the exceedingly high rays of variable width, composed of several rows of thick-walled cells.

tive character. Thus the tracheids lie in two zones. In the outer zone the tracheids form disconnected tracts of variable form and extent, which are rarely connected by a narrow zone of tracheary tissue on the outer face of the growth ring. These tracts are neither radial nor tangential in disposition, but the resultant of these two directions, and as they project diagonally inward, they join with very small vessels which constitute the final phase of such structures in the summer wood. In the second zone of tracheary tissue, the tracheids form tangentially extended tracts of variable form and size which are always connected with vessels of larger dimensions than those lying in the outer zone, and these tracts form an almost continuous series.

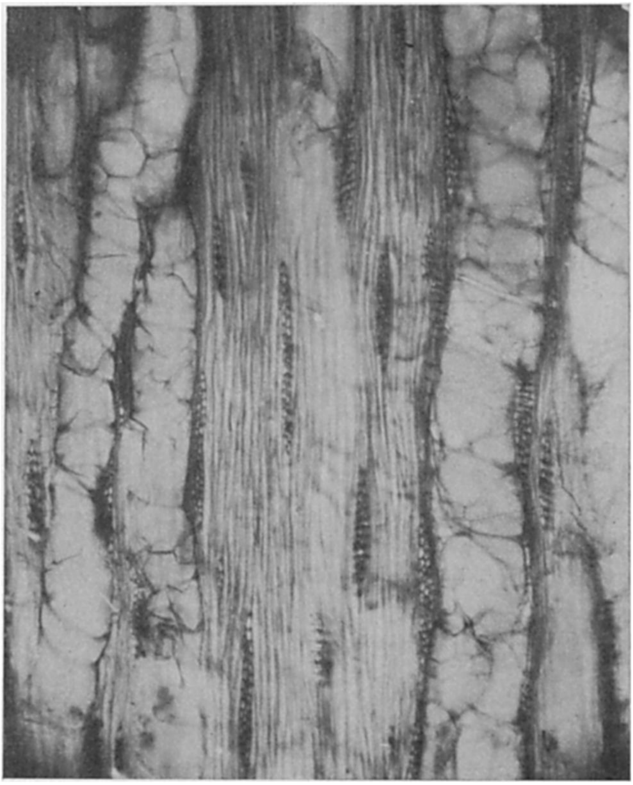

FIG. 8.— *Catalpa bignonioides.* Tangential section, × 61. Showing vessels with numerous thyloses and the medium to rather high, lenticular-oblong rays upwards of three cells wide.

In the hybrid two such zones are also found. The inner zone is composed of tangentially extended tracts of variable form and size centering in vessels corresponding to those of the inner zone of *C. bignonioides* and presenting features which are intermediate between those of the latter species and *C. kæmpferi*. The direct influence of *C. bignonioides* is thus made very apparent. The outer zone of tracheids consists of a limiting layer of rather uniform thickness and generally devoid of vessels. Here and there a tendency to radial extension may be noted, but there is nowhere anything approaching what is to be met with in either *C. kæmpferi* or *C. bignonioides*, and the actual structural condition must be regarded as a resultant from the interaction of these two species, in which a somewhat equal influence appears to have been exerted.

In the radial aspect of structure, the influence of *C. bignonioides* is definitely expressed in the hybrid in (1) the more variable dimensions of the ray cells; (2) in the less coarsely pitted walls; (3) the 2-seriate character of the pits on the radial walls of the tracheids. In the tangential aspect, the influence of the same species is manifested in the thin walls of the ray cells, while the influence of *C. kæmpferi* is expressed in the character of the marginal cells. Other features of a minor character also contribute to the general results thus indicated, a summary of all of which may most conveniently be presented in a tabular view, from which I have excluded all characters common to the hybrid and to the three species.

Comparison of structural variations in Catalpa.

	Teas Hybrid.	*C. kæmpferi.*	*C. bignonioides.*	*C. speciosa.*	No.
Transverse.					
Growth rings very broad	×	×	×	—	3
Growth rings narrow, uniform . . .	—	—	—	×	1
Spring and summer wood obvious . .	—	×	—	×	2
Spring and summer wood not distinguishable or locally defined . . .	×	—	×	—	2
Cells of summer wood uniform, thick-walled, *not at all* in radial rows . .	—	—	—	×	1
Cells of summer wood variable, thin-walled in radial rows	×	×	×	—	3

	Teas Hybrid.	*C. kæmpferi.*	*C. bignonioides*	*C. speciosa.*	No.
Transverse.					
Wood parenchyma confined to the vessels and the earliest spring wood	×	×	×	—	3
Wood parenchyma in tangential and concentric zones of a single layer throughout	—	—	—	×	1
Wood tracheids in radial rows on the outer face of the summer wood, radially extended opposite and confluent with the small vessels	×	×	—	—	2
Wood tracheids forming two zones	×	×	×	—	3
Wood tracheids forming irregular tangential tracts	×	×	×	—	3
Wood tracheids in a terminal layer of 2–3 rows	—	—	—	×	1
Vessels of early spring wood with thyloses	×	×	×	—	3
Vessels of early spring wood without thyloses	—	—	—	×	1
Vessels scattered throughout, often radially compounded	×	×	×	—	3
Vessels very numerous, chiefly small, radially and tangentially compound	—	—	—	×	1
Medullary rays 1–3 cells wide, low to medium, uniform	×	×	×	—	3
Medullary rays 1–5 cells wide, variable	—	—	—	×	1
Radial.					
Upper and lower walls of ray cells finely pitted	×	—	×	×	3
Upper and lower walls of the ray cells coarsely pitted	—	×	—	—	1
Tracheids with hexagonal pits in 1–3 series	—	×	—	—	1
Tracheids with 1–2 seriate bordered pits	—	—	×	—	1
Tracheids with hexagonal, very variable, multiseriate pits	—	—	—	×	1
Tracheids with simple pits in 1–2 rows	×	—	—	—	1
Vessels with multiseriate, hexagonal pits	×	×	×	—	3
Vessels with variable, often much elongated, slit-like pits merging into scalariform structure	—	—	—	×	1
Tangential.					
Rays 1–3 cells wide, low to medium	×	×	×	—	3
Rays upwards of 5 cells wide, unequally multiseriate	—	—	—	×	1
Ray cells small, thick-walled, variable	—	—	—	×	1
Ray cells oblong, thin-walled	×	—	—	—	1
Ray cells hexagonal, thin-walled	—	—	×	—	1
Ray cells hexagonal, thick-walled	—	×	—	—	1
Total characters	15	15	14	13	57

Percentages of characters.

(Those common to all are omitted.)

	Number.	Percent.
Hybrid + bignonioides + kæmpferi	10	31.2
Hybrid + speciosa	0	00.00
Hybrid + bignonioides	1	3.12
Hybrid + kæmpferi	1	3.12
Kæmpferi + bignonioides	0	00.00
Kæmpferi only	3	9.4
Bignonioides only	2	6.24
Hybrid only	2	6.24
Speciosa only	11	34.4
Speciosa + bignonioides	1	3.12
Speciosa + kæmpferi	1	3.
Total	32	99.84

From this percentage summary it appears that *C. speciosa* embodies 34.4 % of characters which are peculiar to itself, while *C. kæmpferi* and *C. bignonioides* possess 31.2 % of characters which are not only common to each other but also common to the hybrid, the remaining characters belonging, with one exception, either to these last two species or to the hybrid. From these facts therefore, we are abundantly justified in the following conclusions: —

1. Hybrid characters are expressed in the structure of the vascular cylinder as well as in external alterations of form and color.
2. *Catalpa speciosa* is not in any way concerned in the production of Teas Hybrid.
3. Teas Hybrid Catalpa is the product of a cross between *C. kæmpferi* and *C. bignonioides*, thus confirming the conclusions already reached by Sargent on the basis of external morphology.
4. The dominant characters of the hybrid, as expressed in the internal structure, are those of the Japanese parent as similarly manifested in the external characters.
5. The resultant characters are most strongly exhibited in transverse section, less so in the tangential, and least of all in the radial.

The question still remains unanswered, as to how far this hybrid approaches and satisfies the conditions which define a species. A complete solution of this question would be obtained in the most satisfactory manner by an anatomical study of reverted forms of the hybrid, were it possible to satisfy all the requisite conditions of authenticity, and determine to what extent the anatomical changes already found to characterize the hybrid, revert to the structure of the separate parents. Unfortunately such studies have not been possible under the conditions of the present investigation, and we are therefore compelled to fall back upon such partial evidence as is afforded by the external morphology. Reference to the original description of the hybrid shows that seedlings exhibit a decided tendency to reversion with respect to the character of the flower, and that such tendency is always in the direction of *C. kæmpferi.* This fact makes it clear that the Japanese parent exerts a dominant influence, while it also shows that the characters are not always fully fixed. Reference to the original description, however, makes it clear that such reversion is not displayed by *all* seedlings but only by *some,* results which are within the limits of justifiable anticipation and in strict accord with Mendel's law. Possibly our knowledge of all the changes incident to reversion is not as yet sufficiently complete to admit of a final expression of opinion as to the actual stability of the hybrid and its status as a species, but it may be kept in mind that while some seeds exhibit reversion, others come true to the hybrid form which is capable of perpetuating itself in succeeding generations. There is in this case no reason for supposing that this is any less a true species than large numbers of plants in which hybridization is an important factor as the starting point for a new line of development. With the abandonment of the old idea of fixity of species, and more particularly in the light of Mendel's law, we are led to see that in any case of hybridization there must be large numbers of progeny which, through reversion, ultimately disappear, while comparatively few acquire such stability as to survive in the form of what must be regarded as definite species. It is only on such grounds that we are justified in regarding as species the numerous and but slightly differentiated forms of the willows, asters, and the Juglandaceæ which Prof. Sargent directs attention to as undoubtedly illustrating the effects of hybridization. Such potential species have always been a source of great difficulty to the systematic botanist who has been unable to properly define their limitations in such a way as to make them recognizable at all times and under all circumstances. The recent separation of six new species of violets from *V. cucullata* by Greene,[1] and the large number of species of Cratægus now recognized by Prof. Sargent can only be explained either as mutant forms or as new species according to the Mendelian law. Their acceptance as valid species shows that our former notions of the relations of hybrids and species have undergone radical change, and that we can no longer accept the limitations which were formerly supposed to be valid. If we are to accept as species those forms only in which there is no reversion to the parental type, and in which there is an absolute fixity of characters, then the hybrid in question cannot be regarded as a species; but if, on the other hand, we accept as species, as is now the custom, those forms which possess strongly defined potentialities, and in which the tendency to reversion is relatively weak, then the hybrid in question must be held to be a valid and distinct species as much as any other plants so defined, and in this sense it should be known as *C. teasi*, n. sp.

It only remains on the present occasion, to define the diagnosis for the genus Catalpa, and present a differential key for the recognition of the species, as follows: —

CATALPA.

Transverse.— Growth rings chiefly broad; the summer wood usually much exceeding the spring but the limitations not sharply defined. Wood parenchyma more or less resinous, often strongly so, generally associated with the vessels but sometimes forming concentric zones. Wood tracheids squarish and forming a limiting layer on the outer face of the growth ring from which irregular tracts may project radially inward, or again form a secondary zone. Vessels numerous, radially or sometimes tangentially compounded, with or without thyloses.

Radial.— Medullary rays somewhat resinous; the cells often higher than long, their upper, lower, and terminal walls rather thick and obviously pitted, their side walls pitted opposite vessels. Tracheids of the limiting zone spiral and scalariform and exhibiting transitions to bordered pits. Wood parenchyma cells variable but narrowly cylindrical, the radial walls with numerous transversely oval, simple pits. The radial walls of the vessels with numerous, multiseriate, hexagonal pits.

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[1] *Ottawa Nat.*, vol. 12, p. 181.

Tangential.— Rays usually numerous and multiseriate, the cells small and thick-walled.

Synopsis of Species.

Resinous wood parenchyma in concentric zones one cell thick.

Vessels of the primary zone large, oval, devoid of thyloses; those of the secondary zone small, very numerous, much compounded.

Rays (tang'l) numerous, low to very high, unequally multiseriate, upwards of 5 cells wide.

Ray cells (tang'l) small, round or oval, thick-walled, variable.

1. *C. speciosa.*

Wood parenchyma sparingly resinous, the cells scattering and chiefly confined to the composition of the vessels.

Vessels chiefly large, not much compounded, scattering and gradually diminishing toward the outer face of the growth ring.

Rays (tang'l) numerous, medium, 1–3 cells wide.

Wood tracheids in two zones; the outer composed of chiefly free, radially diagonal tracts; the inner of rather broad, variable and tangentially extended contiguous tracts forming an almost continuous zone.

Vessels of the primary zone large, oval or round, with few thyloses.

Ray cells (tang'l) thin-walled, hexagonal.

2. *C. bignonioides.*

Rays (tang'l) numerous, low to medium, 1–3 cells wide.

Wood tracheids in one zone, forming a continuous limiting layer with radial extensions opposite small vessels with which they unite, sometimes giving rise to detached groups which thus form a second, discontinuous zone.

Vessels of the primary zone small to medium, round, with strongly developed thyloses, abruptly enlarging in the secondary zone and finally becoming 2–3 compounded radially.

Ray cells (tang'l) rather thick-walled, hexagonal.

3. *C. kæmpferi.*

Wood tracheids in two well defined zones; those of the outer forming a continuous and rather uniform limiting layer upwards of 8 elements thick; those of the inner zone forming a discontinuous tract of variable form and width.

Vessels of the primary zone in a single layer, small with sparingly developed thyloses, becoming abruptly larger and devoid of thyloses in the second zone, and finally sparingly compounded.

Ray cells (tang'l) chiefly oblong, rather thin-walled.

4. *C. teasi*, n. sp.